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VARIATION IN *PARAMYXINE*, WITH A REDESCRIPTION
OF *P. ATAMI* DEAN AND *P. SPRINGERI* BIGELOW
AND SCHROEDER

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No. 11 — *Variation in Paramyxine, with a Redescription of P. atami Dean and P. springeri Bigelow and Schroeder*

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Paramyxine is characterized by having six pairs of external branchial apertures, crowded together towards the posterior end of the branchial region. Consequently, the most anterior efferent branchial ducts are several times the length of the posterior ones (Fig. 2). These characters are sufficient to distinguish *Paramyxine* from *Myxine* and related genera (*Nemamyxine*, *Neomyxine*, and *Notomyxine*) which have only one pair of external branchial apertures, and from *Eptatretus* (= *Bdellostoma*) in which the efferent branchial ducts are of equal length. Two species have been described: *P. atami* Dean 1904, based on a single specimen from 494 m off Cape Manazaru in Sagami Bay, Honshū, Japan, and *P. springeri* Bigelow and Schroeder 1952, based on three specimens taken at 400-600 m in the Gulf of Mexico.

Matsubara (1937) threw doubts on the sufficiency of the description of the type genus and species by demonstrating a considerable degree of variation in a small collection of myxinids taken at about 275 m from Kumano Nada, S.E. of Kii Peninsula, Honshū, Japan. These specimens did not conform completely either to the generic or specific descriptions of *P. atami*, but they were far closer to this species than to any other known forms and Matsubara considered that his specimens were "referable to the above species, although discrepant in several characters" (p. 13). Matsubara was concerned mainly in demonstrating the variation in the arrangement of the branchial apparatus and the teeth, and has left no record of the relative body proportions of his specimens.

Okada et al. (1948a, b) handled almost 1,000 specimens of a myxinid from the commercial hag-fishery of Sado Strait, taken at a depth of 60-160 m, off Niigata, N.W. Honshū, Japan. These authors were more concerned with data of commercial value (sex ratio, weight-length ratio, etc.) than with taxonomic features, and, following Matsubara (1937), they regarded their specimens as referable to *P. atami* even though, for example, the length of the type specimen lay outside the range of their large sample.

Bigelow and Schroeder (1952) have described some features of a specimen from Suruga Bay, S.E. Honshū, Japan (U.S. Nat.

Mus. No. 161442) which they regard (again, in spite of some discrepancies) as referable to *P. atami* Dean. On the basis of this specimen, Dean's (1904) description of the type, and some data from Matsubara (1937), these authors came to the conclusion that their Gulf of Mexico specimens were sufficiently different from *P. atami* to justify the erection of a new species *P. springeri* Bigelow and Schroeder 1952.

Strahan and Honma (1960), in a brief account of the hagfishery of Sado Strait, tabulated the mean body proportions of 50 specimens from a sample of some 500 myxinids collected off Teradomari, N.W. Honshū, Japan. We had overlooked Bigelow and Schroeder's (1952) paper and, somewhat uncritically, had followed Okada et al. (1948a) in regarding our material as typical *P. atami*. We wish now to re-examine the situation in the light of more detailed measurements of some 140 specimens, and with respect to the work of Bigelow and Schroeder.

THE TERADOMARI SAMPLE

The method of collection of the most recent sample has been described by Strahan and Honma (1960). All the specimens were taken on the night of 21/22 October, 1959, at a depth of about 100 m, about 8 miles offshore of Teradomari-machi (near Niigata City), N.W. Honshū, Japan. The animals were maintained in aquaria for 1-3 days and measured under urethane anaesthesia. After measurement, the pituitary glands were removed from the majority of the animals (this being the prime object of the expedition) and the bodies discarded. Some 50 specimens, preserved in formalin, were retained for later examination.

Hagfish are remarkably lacking in taxonomic features susceptible to quantitative formulation. External features that can be studied quantitatively are limited to the over-all length, the number of gill apertures and their position on the body, the position of the cloacal aperture, the number of slime glands and their distribution with respect to the gills and the cloaca. The caudal fin terminates ventrally at the posterior border of the cloaca, but the anterior limit of the dorsal caudal fin is not clearly defined. Similarly, the anterior limit of the ventral (anal) fin is difficult to define. Internal features of taxonomic value are the number and arrangement of the lingual teeth, and the number of gills.

Length. Specimens varied in length from 130 to 583 mm. Hitherto, the longest recorded specimen was the type, 550 mm

long. Matsubara's (1937) specimen was 475 mm long and Okada et al. (1948) did not record any individuals longer than 500 mm. The length frequency of the Teradomari collection is illustrated in Figure 1 and, for comparison, the length frequency histograms of Okada et al. (1948a) are included.

There is a slight difference in the mode of the length in June, August, and October (respectively, 325 mm, 316 mm, and 343 mm) but this may be without significance, particularly since the later measurements are separated by more than a decade from the earlier ones. However, there is a very suggestive increase, from June to October, in the relative frequency of very large individuals (400 mm and more in length).

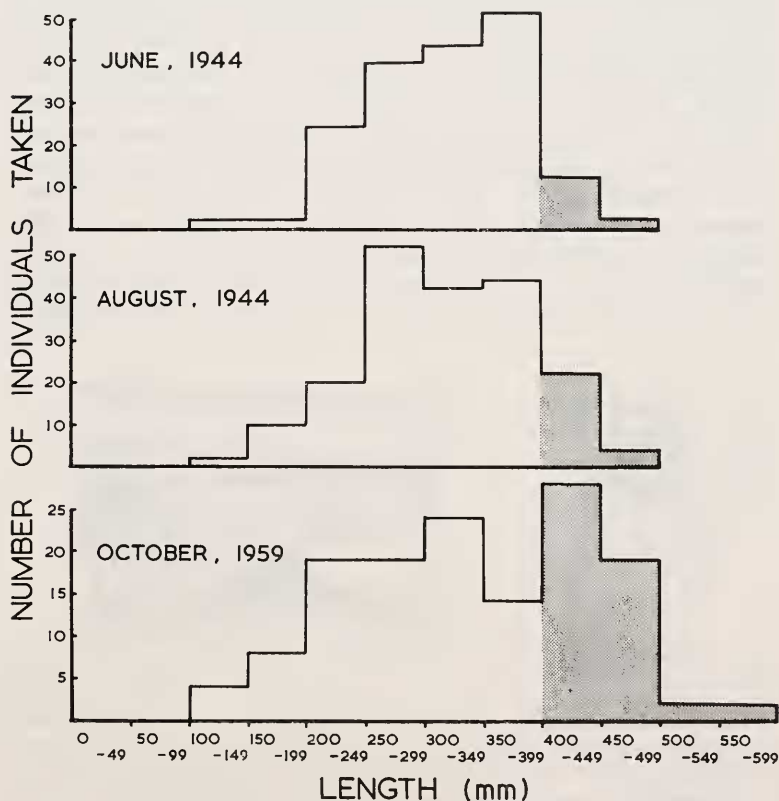


Fig. 1. Length-frequency histogram, *P. atami* taken in the vicinity of Niigata, Japan. Data for June and August, 1944, taken from Okada et al. (1948a). Shaded portions of histogram indicate relative numbers of individuals over 400 mm in length.

Okada et al. (1948b) concluded that spawning occurs off Teradomari mainly in April and May, but that it may extend into August. In late October we found many females with apparently mature eggs. In view of the extreme uncertainty regarding the spawning season (if any) of *Myxine glutinosa* and *Eptatretus stouti* despite extensive and prolonged investigations (see Bigelow and Schroeder, 1948; Conel, 1931), we feel that it is better to leave the question open for the time being.

Branchial system. Dean (1904) defines the genus *Paramyxine* entirely on the branchial system: "Hyperotretes with branchial apertures ventrad of sacs. Ectal branchial ducts of distinctly unequal length, the most anterior several times the length of the most posterior. The duct of the most anterior gill opening at the surface opposite the fourth (or fifth) gill sac. Openings of branchial ducts drawn close together and compressed transversely, that of the ductus oesophagoicus, however, longitudinally, the latter aperture of large size, its length equalling that of the sum of the interspaces of several gills. Transverse constrictor muscles of the branchial region developed as a distinct element in the region of the hindmost branchial sacs." His diagnosis of the species, *P. atami*, adds that there are six gills, that the ectal duct of the most anterior gill is three or more times the length of the most posterior, that the base of the tongue

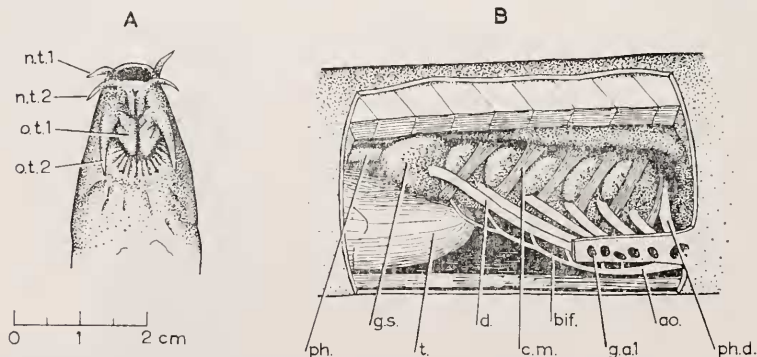


Fig. 2. A. Ventral view of head of *P. atami*, 460 mm long. B. Dissection of left branchial region of *P. atami*, 530 mm long. Abbreviations: *ao.*, ventral aorta; *bif.*, bifurcation of aorta (right branch not shown); *c.m.*, branchial constrictor muscles; *d.*, efferent branchial duct; *g.a.1.*, first gill aperture; *g.s.*, first gill pouch; *nt.1,2*, first and second nasal tentacles; *ot.1,2*, first and second oral tentacles; *ph.*, pharynx; *ph.d.*, pharyngo-cutaneous duct; *t.*, base of 'tongue' muscle.

muscles lies between the third pair of branchial sacs, and that the gill apertures are white against a purplish skin.

The general arrangement of the gill-pouches and ducts in a specimen from Teradomari is shown in Figure 2. It can be seen that this agrees with Dean's description in many respects. However, as Matsubara (1937) noted, there is considerable variation in the position of the posterior end of the lingual musculature. In the individual depicted, this lies between the second pair of gill pouches, but in different individuals its position varies from the first to the fourth gills.

The position of the gill apertures was not recorded by Dean (1904) nor by Matsubara (1937), but we agree with Bigelow and Schroeder (1952) in regarding this as taxonomically significant, although variable. In Tables 1 and 2 the distance from the anterior extremity of the body to the first and to the sixth gill slit is set out as a function of the total length of the animal. There is a definite, though slight, tendency for the branchial

Table 1. Position of the 1st gill aperture in *Paramyxine atami* from Teradomari. Based on 139 specimens.

Total length (mm)	Snout to 1st gill aperture (% of total length)																Arithmetic mean \pm S.D.
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	
100 - 199								2	7	3							29.0 \pm 0.6
200 - 299					1	2	3	8	18	4	0	0	1	0	0	1	28.8 \pm 1.8
300 - 399							4	6	15	10	3						28.1 \pm 1.0
400 - 499	1	0	0	0	1	6	12	10	15	2							27.7 \pm 1.6
500 - 599						2	2										26.5 \pm 0.5
All	1	0	0	0	2	14	23	35	50	12	0	0	1	0	0	1	28.2 \pm 1.6

Table 2. Position of the 6th gill aperture in *Paramyxine atami* from Teradomari. Based on 139 specimens.

Total length (mm)	Snout to 6th gill aperture (% of total length)																Arithmetic mean \pm S.D.
	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	
100 - 199								1	6	3	2						32.5 \pm 0.7
200 - 299					1	1	3	3	12	15	1	1	0	0	0	1	32.3 \pm 1.7
300 - 399							6	11	10	9	1	1					31.8 \pm 0.4
400 - 499	1	0	0	0	1	2	3	9	16	8	2						31.3 \pm 1.7
500 - 599						2	0	1	1								31.2 \pm 1.4
All	1	0	0	0	2	3	19	24	45	36	6	2	0	0	0	1	31.7 \pm 1.5

region to occupy a relatively more anterior position in larger individuals than in shorter ones.

Matsubara (1937) and Strahan and Honma (1960) have drawn attention to the very considerable variation in the arrangement of the external branchial apertures, examples of which are shown in Figure 3. The 12 individuals depicted constitute a random sample which, although it is too small to indicate the relative frequency of particular variations, indicates their type and degree. Matsubara (1937) found only one of his 14 preserved specimens from S. E. Honshu in which the gill apertures were arranged in regular linear series. The remainder showed roughly the same degree of variation as those depicted here. Bigelow and Schroeder (1952) had at their disposal only one specimen of *P. atami* and this, like Dean's type specimen,

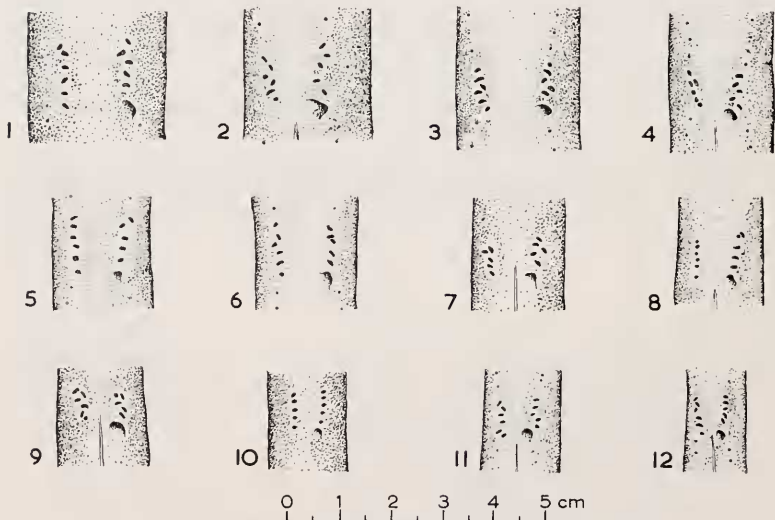


Fig. 3. Variation in arrangement of gill apertures in *P. atami*. Camera lucida drawings of formalin-preserved specimens.

had the gill openings regularly and evenly aligned. Commenting upon Matsubara's observations, these authors suggest that the irregularities may be due to muscular contraction. We are convinced that this is not so, since we have observed quite irregular arrangements in heavily anaesthetised animals. On the other hand, we agree with Matsubara (1937) in his suggestion that the outline of the apertures is liable to change during

preservation. In the living animal, the apertures may be more or less circular, triangular, or elongately oval, but the outline is smoothly convex. After preservation in formalin, the more elongate apertures may develop crenellations and become crescentic. However, if such specimens are placed for a time in water, the turgor developing from osmotic inflow restores a condition similar to that in life. The specimens depicted in Figure 3 were so treated.

Dean (1904) regarded the transverse orientation as a generic character. In common with Matsubara (1937) and Bigelow and Schroeder (1952), we find that the variation is too great to sustain this opinion. Similarly, we must reject Dean's criterion of a longitudinally elongated aperture to the pharyngo-cutaneous duct ("ductus oesophagoeus"). The pharyngo-cutaneous duct and sixth branchial aperture communicate with a shallow common depression, partially covered by a more or less semicircular fold of skin, and directed postero-mesially. The arrangement is not particularly variable and we have found no example of a markedly longitudinal depression. We can, however, confirm that the gill apertures have unpigmented borders.

In a number of individuals (Fig. 3, Nos. 7 and 10) there are only 5 gill apertures on the right-hand side of the body, and we have seen one individual in which there were only 4. The left-hand side is less variable in this respect, although one individual was found with 7 apertures on this side, due to separate opening of the 6th efferent branchial duct and the pharyngo-cutaneous duct. The existence of 5 apertures does not necessarily imply that there are only 5 gill pouches. Dissection of three individuals with 5 apertures on the left side revealed 5 gill pouches in one individual and 6 in the other two, the latter having one of the apertures shared by two adjacent ducts.

The cloaca. The cloaca is slit-like, as in *Myxine*, and surrounded by slightly swollen lateral lips. The ventral caudal fin arises immediately posterior to the cloaca, and we have therefore used the posterior border of the cloaca as a measurable landmark for this structure. The ventral (anal) fin terminates just anterior to the cloaca.

As can be seen from Table 3, the cloaca occupies a relatively more posterior position in longer individuals. Since the branchial region is relatively more anterior and the cloaca relatively more posterior in longer specimens, the length of the abdomen is quite markedly increased, and this is consequently a poor taxonomic character.

Slime glands. The slime glands, where they occur, are segmentally arranged, one per myotome. The linear series begins at the fourth or fifth myomere and extends back to the myomere immediately in front of the 1st branchial aperture. A second series begins at the level of the first postbranchial myomere and continues to the region of the cloaca where there is a gap, representing from one to four myomeres, after which a third series continues for about ten myomeres up to the region of the caudal heart. Thus, the slime glands may be divided into a prebranchial, an abdominal, and a caudal series.

Table 3. Position of the posterior border of the cloaca in *Paramyxine atami*. Teradomari sample. Based on 136 specimens.

Total length (mm)	Snout to posterior border of cloaca (% of total length)												Arithmetic mean \pm S.D.	
	81	82	83	84	85	86	87	88	89	90	91	92		
100 - 199						6	0	5						86.9 \pm 1.0
200 - 299	1	0	0	0	1	7	8	17	3					87.2 \pm 1.4
300 - 399					3	1	7	16	9	2				87.9 \pm 1.2
400 - 499							7	19	15	3	1	1		88.5 \pm 1.0
500 - 599							1	0	3					88.5 \pm 0.8
All	1	0	0	0	4	14	23	57	30	5	1	1		87.8 \pm 1.1

The mean values for the three series and for the total number are set out in Table 4. There is no correlation between the number of slime glands and the total length. This is perhaps to be

Table 4. No. of slime glands in left side of body of *Paramyxine atami* from Teradomari. Based on 123 specimens.

Total length (mm)	Mean No. of Slime glands			
	Prebranchial Series	Abdominal Series	Caudal Series	Total No.
100 - 199	18.8 \pm 0.9	45.0 \pm 1.4	11.3 \pm 0.8	75.7 \pm 2.0
200 - 299	18.6 \pm 1.3	44.9 \pm 2.2	11.0 \pm 1.0	74.5 \pm 2.6
300 - 399	18.9 \pm 1.5	44.6 \pm 1.9	10.9 \pm 0.9	74.7 \pm 2.5
400 - 499	18.9 \pm 1.0	45.1 \pm 1.4	10.8 \pm 0.9	74.9 \pm 2.2
500 - 599	19.3 \pm 0.9	47.3 \pm 0.9	11.5 \pm 1.1	77.7 \pm 1.3
All	18.8 \pm 1.2	45.0 \pm 1.9	10.9 \pm 1.0	74.9 \pm 2.6

expected if the number of slime glands is determined by the number of myomeres. The total number of slime glands is fairly constant, 95 per cent of the specimens examined having a total number of slime glands falling within two standard deviations of the arithmetic mean (71-79). The division of the glands into three linear series is more variable. Of the sample of 123 individuals, only 3 have the arrangement suggested by the means of each series (prebranchials 19: abdominals 45: caudals 11), but 78 (63%) fall within one standard deviation of these means (prebranchials 18-20: abdominals, 43-47; caudals 10-12), and 121 (98%) fall within two standard deviations (prebranchials, 16-21: abdominals 41-49: caudals 9-13).

Caudal fin. In our original description (Strahan and Honma, 1960, p. 29) we stated that "the dorsal caudal fin has no clearly-definable origin, but may be said to arise at approximately the level of the anterior border of the cloaca." However, Bigelow and Schroeder (1952) state that their specimen of *P. atami* has a dorso-caudal fin extending as far forward as the 6th pair of gill apertures, although it is only a low ridge. These authors also draw attention to Matsubara's (1937) illustration, which shows a dorsal fin of about the same height as the ventral fin, extending forwards to what they estimate as "one-third to one-half the distance from the level of the cloacal pocket toward the level of the 6th pair of gill openings," i.e., about 60 per cent of the length of the body from the snout. Unlike the ventral (anal) fin, the dorsal caudal fin is supported by fin-rays, and its limits may be specified in terms of the distribution of these structures. We skinned a small number of specimens and found a series of dorsal fin rays extending anteriorly to about 65 per cent of the body length from the tip of the head (see Table 5).

The difference between the apparent and real origin of the dorsal caudal fin, i.e., the position of the most anterior fin-ray and the point at which the fin becomes obvious as a thin membrane distinct from the rounded contour of the body, is due to several factors. The fin-rays anterior to the level of the cloaca are short and inclined strongly towards the horizontal. Between them and the skin of the fin is considerable fatty connective tissue which masks the discontinuity between the fin and the body proper. It is unlikely that this part of the fin is very much more prominent in life, for the skin here is thick and tough.

The caudal fin is continuous around the tail and extends forward ventrally as far as the posterior border of the cloaca. The fin-rays in the ventral part of the caudal fin are unbranched, in contrast to those in the dorsal and terminal part.

Table 5. Real and apparent anterior limits of the dorsal fin, based on 8 skinned specimens of Paramyxine atami.

Total length (cm)	Apparent origin Distance from snout		Most anterior fin-ray Distance from snout		Number of rays
	(cm)	% Total length	(cm)	% Total length	
139	112	80	93	67	-
191	160	84	130	68	51
278	225	81	175	63	53
291	241	83	186	64	56
295	245	83	183	62	63
310	254	82	207	67	48
353	295	84	228	65	61
355	300	85	227	64	66
Mean \pm S.D.		83 \pm 1		65 \pm 1	57 \pm 7

Bigelow and Schroeder (1952) found a difference in the configuration of the ventral border of the caudal fin in *P. atami* and *P. springeri*. They state (p. 4) that it is "nearly straight in all three of the Gulf of Mexico specimens while it is pictured as moderately convex in the two Japanese specimens of *atami* which have been illustrated (Dean 1904, pl. 1, fig. 3; Matsubara 1937, pl. 1, fig. A), likewise in the National Museum specimen of *atami* (compare Fig. 5 with Fig. 6)." We do not find this to be a specific character. In Figure 4, we have depicted the caudal fins of ten randomly-selected individuals. These show slight convexity and concavity, but are no less straight than that of *P. springeri* (Fig. 4, no. 11). The posterior part of the fin has a white border, one to two mm deep.

The ventral fin. In anaesthetized animals, it is difficult to determine the anterior limit of the ventral (anal) fin. The shrinkage caused by preservation renders the fin more conspicuous, but it does not permit very accurate localisation of the junction between the thin fin and the thick ridge running along the mid-ventral surface of the abdomen. In a sample of 42 preserved specimens, we estimate the anterior border of the

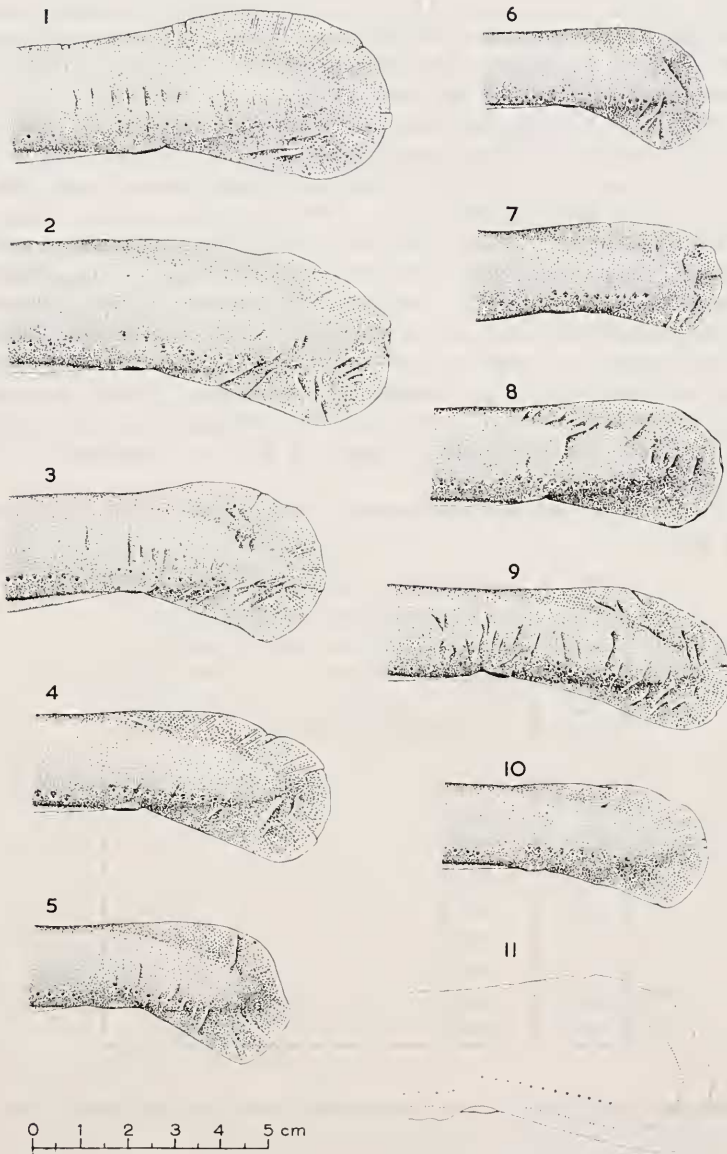


Fig. 4. Contour of the caudal fin in *Paramyxine*. Nos. 1-10, *P. atami*, camera lucida drawings of formalin-preserved material. No. 11, *P. springeri* (after Bigelow and Schroeder, 1952). Note variation in the arrangement of the slime glands.

ventral fin to be situated $47.3 + 2.7$ per cent of the total length of the body from the anterior tip. This value ranges from 39 per cent to 54 per cent; but we find no correlation between this and the length of the body.

The lingual teeth. The procedure for dissecting the pituitary of the animal involved splitting the dental skeleton longitudinally. The teeth of the left side only were counted and thus we have no data on the degree to which asymmetry may occur. The teeth were counted under a binocular microscope, care being taken to lift away the skin fold covering the outermost teeth of each row. The frequency distribution of the various combinations of teeth on the outer and inner combs (see Table 6) is much the same as that published in our earlier paper, but is based on a larger number of specimens. It may be noted that the range does not come near to including 13 outer: 12-13 inner, which is the dental formula of the type specimen of *P. atami*.

There is no correlation between total length and the number of teeth.

Table 6. Arrangement of lingual teeth in *Paramyxine atami* from Teradomari. Based on 109 individuals.

Number of teeth		Number of individuals	Percentage of individuals
Outer row	Inner row		
8	10	1	1
9	9	13	12
9	10	9	8
10	9	10	9
10	10	55	50
11	11	4	4
11	9	2	2
11	10	9	8
11	11	5	5
12	10	1	1

DIFFERENCES BETWEEN SPECIMENS FROM THE EAST AND WEST COASTS OF JAPAN

Records of the occurrence of *Paramyxine* have been collated by Strahan and Honma (1960). On the Pacific coast of Honshū it has been recorded from Aomori Province (Matsubara, 1955),

Ibaragi Prefecture (Asano, 1956), Sagami Bay (Dean, 1904), Suruga Bay (Bigelow and Schroeder, 1952), Kii Peninsula (Matsubara, 1937), and Kōchi Prefecture (Kamohara, 1952). On the east coast of Honshū, there are records from the vicinity of Niigata (Okada et al., 1948a, b; Strahan and Honma, 1960), and from San-in District (Mori, 1956). Mori (1952) includes *P. atami* in a check-list of Korean fishes.

There seems to have been no attempt to compare these specimens in detail with the type, except in the case of Bigelow and Schroeder who, like Dean, were limited to one specimen. Since the Teradomari sample differs in several characteristics from the type and from the U.S. National Museum specimen, both of which are from the east coast of Honshū, we tried to get a sample of *Paramyxine* from the Pacific coast of Japan, but have been able to obtain only five specimens, from Kanbara, in Suruga Bay. These are similar in body proportions to the U.S. National Museum specimen (also from Suruga Bay) and they have been grouped together with it for comparison with the Teradomari sample, the type, and the specimens from the Gulf of Mexico (Table 7).

Table 7. Taxonomic characters of *Paramyxine* populations from the east and west coasts of Honshu, and from the Gulf of Mexico.

Character	Western Japan	Eastern Japan		Gulf of Mexico
	Teradomari (120 - 140)	Suruga Bay (6)	Sagami Bay (1)	
Snout to 1st gill aperture (% T.L.)	28.2 ± 1.6	26.6 ± 1.0	25.5	23.1 ± 0.4
Snout to 6th gill aperture (% T.L.)	31.7 ± 1.5	29.9 ± 1.2	27.9	26.6 ± 1.0
Snout to post border cloaca (% T.L.)	37.8 ± 1.1	37.1 ± 0.3	35.5	35.2 ± 1.7
No. prebranchial slime glands	18.8 ± 1.2	16.6 ± 1.1	17-20 ? ²	17.3 ± 1.7
No. abdominal slime glands	45.0 ± 1.9	45.5 ± 1.1	58 ? ²	52.3 ± 5.5
No. caudal slime glands	10.9 ± 1.0	9.0 ± 1.1	10 ? ²	12.2 ± 1.0
Total no. slime glands	74.9 ± 2.6	71.0 ± 2.1	? ²	86.0 ± 5.6
Mean no. teeth, outer row	10.0 ± 0.7	11.5 ± 0.5	13	13.5
Mean no. teeth, inner row	10.0 ± 0.6	11.5 ± 0.5	12.5	11.5

1. Figures in brackets under place names indicate size of sample.
2. Dean's two illustrations are not in agreement with each other.

With respect to all the characters set out in Table 7 (except the number of abdominal slime glands), the specimens from Suruga Bay are significantly different from the Teradomari sample (difference between the means is of the order of three times the sum of the standard error of the means). In spite of

the small size of the Suruga Bay sample, this indicates a biological difference between the two populations, although this is probably not so great as to warrant sub-specific distinction, since the joint non-overlap (Mayr, Linsley and Usinger, 1953) of the most divergent character (no. of lingual teeth) does not exceed 89 per cent.

Data on the type specimen are rather unreliable. The only measurement given by Dean (1904, p. 14) is the total length (about 550 mm). Bigelow and Schroeder (1952) attempted to derive the dimensions from Dean's figures, but the figures themselves are suspect, particularly with respect to the slime glands, which Dean regarded as too variable to be of taxonomic value. The measurements given for the type specimen in Table 7 are calculated from Dean's (1904) text-figure 2 and plate I, fig. 3. Insofar as any reliance can be placed on them, they indicate that the branchial region is even more anterior than in the Suruga Bay specimens, while the cloaca is even more anterior than in the Teradomari sample. The number of abdominal slime glands appears to be considerably greater in his specimen than in other Japanese *Paramyxine*. Nevertheless, there is insufficient evidence to separate this single specimen from others that we have examined. The Teradomari sample included a specimen with body proportions fairly similar to the type (250 mm long; snout to 1st gill aperture, 26%; snout to 6th gill aperture, 28%; snout to posterior border of cloaca, 89%; pre-branchial slime glands, 16; abdominal slime glands, 51; caudal slime glands, 11), so it seems that the type may be regarded as atypical, but within the range of variation which has been demonstrated.

THE VALIDITY OF *P. SPRINGERI*

Once the type description is questioned, the validity of the separation of *P. springeri* from it must also be reviewed. However, reference to Table 7 shows that the specimens from the Gulf of Mexico differ from the Teradomari and Suruga Bay populations even more than they do from the type specimen. There is a significant difference between the means of all the characters tabulated for the Teradomari and American forms, and the percentage of non-overlap is high for many of the characters (snout to 1st gill aperture, snout to 6th gill aperture, total number of slime glands, and number of lingual teeth), exceeding 96 per cent. This, in itself, is probably only enough

to justify separation into subspecies. There is, however, a further difference between *P. atami* and *P. springeri* which permits a clear separation. This is the presence in *P. springeri* and the absence in *P. atami* of slime glands in the branchial region. As mentioned above, the prebranchial series of slime glands in *P. atami* is clearly separated from the abdominal series by a gap in the region of the branchial apertures. In *P. springeri* there is a short series of glands in the branchial region, running parallel to, and on the ventro-mesial side of the line of the gill apertures. In the three specimens of *P. springeri* which have so far been described, the number of glands in the "branchial" series varies from 3 to 6.

DISCUSSION

Dean (1904, p. 18) states, "The wide range in the variational characters in species of myxinoids has long been appreciated, in the matter, for example, of the number of gills and 'teeth' and in the proportions of body regions and fins. My own observations lead me to the belief that in the case of myxinoids it is peculiarly necessary to base specific determinations upon the average characters of as great a number of individuals as practicable." Similar views have been expressed by Ayers (1894, *vide* Worthington) and Worthington (1905), who worked on the Californian *Eptatretus*, and by Bigelow and Schroeder (1948) in their review of the reputed species of *Myxine*. However, no authors have hitherto presented a simple analysis of variation within a myxinid population, expressed in terms of mean values of quantitative characters and the standard deviations of these means. Without such treatment, and quantitative consideration of the degree of overlap of different populations, there is very little that can be usefully said on the subject.

Our analysis makes it clear that there is a significant difference between *P. atami* from Teradomari and *P. atami* from Suruga Bay. From this, we have deduced the existence of an eastern and a western form of the species. Proof of this would require more widespread sampling, to determine, for instance, whether the populations intergrade with each other around the north and south coasts of Honshū, or whether there is discontinuous variation. There is a possibility of a cline extending from the Sea of Japan to the Gulf of Mexico. It is dangerous to assume this on three samples, two of which are rather small, but examination of Table 7 suggests that such a cline may involve

a progressive shortening of the prebranchial region and an increase in the number of lingual teeth from west to east over the range of the genus.

The type specimen of *P. atami* is incompletely described, and the diagnosis of the genus and species has been shown to be at fault in several respects. We therefore propose a further description of the genus and species, and a simplified description of *P. springeri*. The latter is based entirely upon the excellent description of Bigelow and Schroeder (1952) and differs from it mainly in selection of those characters which we regard as taxonomically significant.

PARAMYXINE Dean 1904

Myxiniformes characteristically with 6 gills with separate efferent branchial ducts of distinctly unequal length, the most anterior being more than twice the length of the most posterior, opening separately to the exterior, except for the most posterior on the left side, which opens into the same external aperture as the pharyngo-cutaneous duct. External branchial apertures lying close together in the posterior third of the branchial region, the series on the two sides converging rearwards in a linear or irregular arrangement.

Rostral flap above nasal aperture wider than long, nasal aperture relatively larger in diameter than in *Myxine*. Distal ends of second pair of oral tentacles bluntly rounded.

Dorsal caudal fin apparently originates at level of cloaca (but fin rays may extend farther forward), continuous around posterior tip of body to posterior border of cloaca, ventral edge of fin more or less straight. Ventral (anal) fin extends from anterior border of cloaca to about 40 per cent of the length of the body from the snout.

Body darker on back and sides than ventrally, edges of caudal and anal fin and tips of tentacles paler than surrounding skin. Branchial apertures with white borders. Distinct pale patch over region of eye.

Up to about 60 cm in length.

PARAMYXINE ATAMI Dead 1904

Six gills (rarely five on right side), external branchial apertures in two irregular (rarely regular) rows on ventral surface. Snout to first gill aperture 28.2 ± 1.6 per cent of total length

(western form) or 26.6 ± 1.0 per cent (eastern form). Snout to posterior border of cloaca 87.8 ± 1.1 per cent of total length (western form) or 87.1 ± 0.3 (eastern form). Slime glands 18.8 ± 1.2 prebranchial, 45.0 ± 1.9 abdominal, 10.9 ± 1.0 caudal (western form). Slime glands 16.6 ± 1.1 prebranchial, 45.5 ± 1.1 abdominal, 9.0 ± 1.1 caudal (eastern form). Total number slime glands 74.9 ± 2.6 (western form) or 71.0 ± 2.1 (eastern form). No slime glands in region of branchial apertures. Lingual teeth, 10 ± 0.7 outer, 10 ± 0.6 inner (western form) 11.5 ± 0.5 outer, 11.5 ± 0.5 inner (eastern form).

Color, purplish-brown dorsally and laterally, grey ventrally. Length, up to 58 cm. Coastal waters of Honshū (Japan), Korea.

PARAMYXINE SPRINGERI Bigelow and Schroeder 1952

(Simplified Description for Comparison with *P. atami*)

Six gills, external branchial apertures in two rather regular rows on ventral surface. Snout to 1st gill aperture 23.1 ± 0.4 per cent of total length. Snout to posterior border of cloaca 85.2 ± 1.7 per cent. Slime glands 17.3 ± 1.7 prebranchial, 52.3 ± 5.5 abdominal, 12.2 ± 1.0 caudal. Total number of slime glands 86.0 ± 5.6 . Slime glands on each side, ventro-mesially to external branchial apertures. Lingual teeth 13-14 outer, 11-12 inner. Color, greyish-brown. Gulf of Mexico.

SUPPLEMENTARY NOTE

Teng (1958) has recently described a new species, *P. yangi*, eight specimens of which have been obtained from fish markets in Kaohsiung, Taiwan, and are assumed to have been caught in waters to the southwest of Taiwan. *P. yangi* is characterised by having only 5 pairs of gills and external branchial apertures, arranged irregularly as in *P. atami*. The head is longer than in *P. atami* or *P. springeri*. A summary of the major characteristics is given below.

	Mean and Standard Dev.	Range
Total length (T.L.)	229 ± 6 mm	(198-250 mm)
Snout to 1st branchial aperture (% T. L.)	31.7 ± 1.3	(28.9-32.9)
Snout to 5th branchial aperture (% T.L.)	33.3 ± 1.0	(30.7-34.9)
Snout to post. border of cloaca (% T.L.)	86.0 ± 1.8	(81.2-87.6)
No. prebranchial slime glands	18.1 ± 1.0	(17-20)
No. abdominal slime glands	37.1 ± 1.5	(35-40)
No. caudal slime glands	8.6 ± 1.1	(8-10)
Total no. slime glands	63.8 ± 2.8	(60-69)

Key to species of *Paramyrxine*

- 1a. Five pairs of gills; snout to 5th branchial aperture about 33% of total length; about 65 slime glands on each side; number of abdominal slime glands approximately twice the number of prebranchial slime glands; slime glands absent between 1st and 5th branchial apertures; 9-10 lingual teeth in internal row, 9-10 in external row; up to 250 mm in length. *yangi* Teng, 1958. Taiwan.
- 1b. Six pairs of gills.
- 2a. Snout to 6th branchial aperture about 30% of total length; about 75 slime glands on each side; number of abdominal slime glands approximately 2.5 times the number of prebranchial slime glands; slime glands absent between 1st and 6th branchial apertures; 9-10 lingual teeth in internal row, 9-10 in external row; up to 583 mm in length. *atami* Dean, 1904. Japan.
- 2b. Snout to 6th branchial aperture about 27% of total length; about 85 slime glands on each side; number of abdominal slime glands approximately 3 times the number of prebranchial slime glands; 3-6 pairs of slime glands between 1st and 6th branchial apertures; 11-12 lingual teeth in internal row, 13-14 in external row; up to 590 mm in length. *springeri* Bigelow and Schroeder, 1952. Gulf of Mexico.

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SUMMARY

Variation in the taxonomic characters of *Paramyrxine atami* Dean from the eastern and western coasts of Japan is described. These populations differ significantly (in the position of the branchial region, the number of prebranchial and caudal slime glands, and the number of lingual teeth), but not sufficiently to

rank as subspecies. The type specimen is not typical of either population and appears to be an unusual specimen. Certain points in the original definitions of the genus and species are invalid and further descriptions are given. *P. springeri* Bigelow and Schroeder, from the Gulf of Mexico, is found to be taxonomically distinct from *P. atami*, particularly in possessing slime glands in the branchial region. A simplified diagnosis of *P. springeri* is given. A note on the recently described species, *P. yangi* is appended, with a key for separation of the three species of *Paramyxine*

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